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POPULATION CHARACTERISTICS OF A CLOSED NORTHERN PIKE (*ESOX LUCIUS*) CATCH-AND-RELEASE POPULATION IN MINNESOTA

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John Kempe

Freshwater fisheries are typically open to exploitation, and are often a major part of local economies. Overexploitation is becoming increasingly common with new technologies, resulting in loss of genetic diversity, altered food webs and declines in angler catch rates. Population dynamics of unexploited freshwater fish populations are rare, and offer insight into how a natural aquatic ecosystem functions. Shingobee Lake has been closed to the harvest of Northern Pike since 2005, and had a long-term tagging study in place from 2009-2017. The length of the study, lack of exploitation and high tagging percentage (37-59%) provide a unique insight into the population dynamics of a catch-and-release Northern Pike population. The Northern Pike population in Shingobee Lake is female dominated and consists of large, slow growing individuals with low mortality rates. Abundance estimates throughout the study period remained stable (21-33 fish/ha) and a catch curve indicated an overall mortality rate of 31%. Growth rates were slower than the international growth standard and inter-annual weather patterns did not influence growth as much as fish density. Proportional stock density ranged from 42-58 demonstrating a stable size structure. Restricting Northern Pike fishing to catch-and-release only improved the size structure and protected large, older individuals.

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Chapter 1: Literature review of the impacts of exploitation on freshwater fisheries

Most North American freshwater fisheries are overexploited and the few that are lightly exploited or unexploited are the result of remoteness or access limitation (Post et al. 2002). Exploitation of fisheries can substantially impact populations through changes in abundance, size-structure, and life history traits (Healy 1978, 1980; McDonald and Hershey 1989; Paukert and Willis 2001). Fishery management theory is based on a nonlinear relationship between stock size and recruitment (Ricker 1975), such that maximum yield from a fishery occurs at a stock size below the unexploited population (Healy 1980). It assumes that compensatory effects (e.g., increased fecundity, increased growth rate, deceased age at maturity) occur through reductions in intraspecific competition when angling lowers the abundance of the population (Beard et al. 1997). However, the effect of compensatory mechanisms may be offset by loss of genetic diversity (Lewin et al. 2006), truncation of the natural age and size structure (Beard and Kampa 1999, Radomski 2003) and an altered food web (Post et al. 2002). Another concern regarding fish populations is their ability to rebound after intense exploitation has stopped. Post at el. (2001) documented the inability of Canada's populations of Walleye *Sander vitreus*, Rainbow Trout *Oncorhynchus mykiss*, Lake Trout *Salvelinus namaycush* and Northern Pike *Esox lucius* to rebound after intensive exploitation.

Fisheries previously closed to angling are susceptible to high exploitation when opened to angling for the first time. Goedde and Coble (1981) reported removal of an estimated 35, 74, 86, 53 and 46% of Bluegill *Lepomis macrochirus*, Pumpkinseed *Lepomis gibbosus*, Yellow Perch *Perca flavescens*, Largemouth Bass *Micropterus salmoides* and Northern Pike respectively in Mid Lake, Wisconsin within a month of the fishery opening, with half of the exploitation occurring within the first two days. Schneider (1973) found similar results with exploitation rates of 13, 29, 61, and 35% of Bluegill, Pumpkinseed, Yellow Perch and Largemouth Bass respectively in five days after Mill Lake, Michigan was opened to angling. Redmond (1974) estimated exploitation rates of 39 to 66% for Largemouth Bass in the first three days five lakes in Missouri were open to angling. Walleye exploitation rates were 75% in Hazeldon Lake, South Dakota within the first month and a half when opened to fishing (Blackwell et al. 2013). In a study of a small boreal lake in Ontario, Canada, Mosindy et al. (1987) reported fewer than 450 angler-hours of effort (1.24 angler-hours/hectare) removed 43 and 50% of the estimated annual adult production of Walleye and Northern Pike, respectively.

Unexploited fisheries typically have a large proportion of their population consisting of large, old fish with low total mortality rates (Goedde and Coble 1981; Donald and Alger 1986; Mosindy et al. 1987; Reed and Rabeni 1989). Reed and Rabeni (1989) compared mortality rates of Smallmouth Bass *Micropterus dolomieu* in unexploited and exploited Missouri streams. Total annual mortality ranged from 11-16% in unexploited streams and 41-66% in exploited streams. A study in Wisconsin by Goedde and Coble (1981) comparing the effects of angling on a previously unfished lake showed mortality rates of Pumpkinseed to increase from 42 to 83% after fishing began. Healy (1975) studied how exploitation effected Whitefish *Coregonus clupeaformis* populations in the Northwest Territories of Canada by grouping lakes into three categories: heavily exploited, moderately exploited or lightly exploited. Mean mortality rates of the grouped lakes were 79, 68 and 47%, respectively. In unexploited Murray

Lake, Diana (1983) calculated a Northern Pike mortality rate of 28% compared to a rate of 85% for heavily exploited Houghton Lake. Healy (1975, 1980) and Diana (1983) also showed as mortality increases, fish mature at a younger age.

Fisheries experiencing overharvest result in a decreased age at maturity due to a shift in energy from growth to reproduction (Meyer et al. 2003). Age at maturity of a fish population influences population model estimates of sustainable harvest rates and can also be a predictor of overexploitation. High mortality due to fishing decreases the probability of a fish surviving beyond a couple years; reducing the number of times a fish can spawn in its lifetime (Trippel 1995). Miller (1947, 1956) showed prior to increased fishing pressure on Whitefish in Pigeon Lake, Alberta, only a few fish spawned when three years old, but most were mature at four years. After an increase in fishing pressure, all of the two-year-old fish became mature, indicating a dramatic decline in age of maturity associated with increased fishing pressure. Whitefish analyzed by Kennedy (1953) in Great Slave Lake, Canada first matured at five years old with 50% of the population mature at nine years. After the fishery was exposed to heavy exploitation, Bond and Turnbull (1973) reported fish first maturing at four years old, with 50% of the population mature at age six. Age at maturity reductions were shown in Lake Erie by Wolfert (1969) comparing maturation of Walleye in 1927-28 with data from 1964-66. In the earlier period, female Walleyes matured at ages four and five and male Walleyes matured at three and four. During the later period, with increased exploitation and an accelerated growth rate, 85% of the females were mature at age three and 99% of the males matured by age two. Yellow Perch showed a similar change in maturation on Lake Erie, with the majority of females spawning for the first time shifting from age three during 1927-37 to age two during 1960-66 (Spangler et al. 1977). Diana (1983) showed female Northern Pike in Michigan maturing at an earlier age when exposed to heavy exploitation, along with higher total energy allocations to reproduction.

Truncated age and size distributions are another common result of fish populations being over exploited (Radomski 2003). Olson and Cunningham (1989) analyzed fishing contest records of exploited fish species in Minnesota and observed a long-term decline in large individuals of Northern Pike, Muskellunge *Esox masquinongy*, Walleye, Largemouth Bass, Bluegill, and Black Crappie. In the absence of exploitation, growth and mortality are regulated by density dependent (Ricker 1975) and abiotic (e.g. temperature) factors. Growth has been shown to be slower in unexploited fish populations of Smallmouth Bass (Reed and Rabeni 1989), Brook Trout *Salvelinus fontinalis* (Toetz et al. 1991), Walleye (Craig et al. 1995) and Northern Pike (Goedde and Coble 1981) when compared to exploited populations. For example, the growth rates of female Walleye in Lake Erie from 1927-33 (18 cm at age 2; Deason 1933) were considerably slower compared to 1964-66 (37 cm at age 2; Parsons 1972), a period of increased exploitation. The result of removing large individuals may increase the growth rate of juvenile fishes through reduced intraspecific competition at lowered population abundances. However, because fish size correlates with many reproductive traits, the selective removal of large individuals may affect the reproductive capacity of the exploited fish population (Lewin et al. 2006).

Fish size correlates with many reproductive traits and the removal of large individuals may affect the reproductive potential of a population. Egg size has been shown to increase with age, size, or weight of a fish in populations of Walleye (Johnston

1997), Brown Trout *Salmo trutta* (Olsen and Vollestad 2001), Yellow Perch (Lauer et al. 2005), and Northern Pike (Wright and Shoesmith 1988). Larger egg size often increases larval size and early growth (Wallace and Aasjord 1984) positively influencing the probability of survival to maturity. Older fish often have a higher hatching success than first time spawners (Trippel 1998), commonly attributed to factors such as ideal spawning time or egg size and quality. Fish age influences reproductive success in certain species due to a competitive advantage enabling them to obtain better spawning sites, or as in the case of salmonids, to dig deeper redds (Van den Berghe and Gross 1984). Fish age also influences the time of spawning. Smaller and younger fish may spawn later than larger, older fish because they emerge from the winter with lower lipid reserves and insufficient energy (Lewin et al. 2006). Hatch rate, resistance to starvation and survival rate were significantly higher for Northern Pike eggs spawned earlier compared to eggs spawned later (Trabelsi et al. 2012). Miranda and Muncy (1987) found an earlier hatch rate in Largemouth Bass resulted in increased size in young-of-year bass, and recruitment of a larger portion of the cohort into the fishery. Heyer et al. (2001) suggested a natural and variable age structure improves recruitment and enhances the population’s resilience to external disturbances. In fish species with long life spans, a diverse age structure can be seen as a bet-hedging strategy that ensures reproductive success of at least some individuals under variable environmental conditions (Secor 2000).

Old, large fish species are successful due to “cultivation effects”, where they crop down forage species competing and/or preying on juveniles of their own species (Walters and Kitchell 2001). Lowering the abundance of these old, large fish may reduce top-down control on smaller species and impair their potential for compensatory responses

(Lewin et al. 2006). Changes in abundance of top predators play a significant role in the trophic interactions that regulate zooplankton community structure, algal dynamics and nutrient cycles in freshwater ecosystems (Brett and Golman 1996; Finlay et al. 2005). Under heavy exploitation, Walleye populations in Alberta, Canada, have shown persistent recruitment failure, accompanied by dramatic increases in minnow populations thought to prey heavily on Walleye larvae (Post et al. 2002). The structure of aquatic food webs along with the influence of environmental factors may facilitate compensatory responses, which make it difficult to predict the outcome of changes on a top predator level. However, given that fishermen typically exploit top predators, it can be assumed that angling has the potential to affect the trophic structure and thereby alter aquatic ecosystems (Lewin et al. 2006).

Studies concerning angling related consequences on the aquatic environment to date have mainly focused on commercial fisheries (Cooke and Cowx 2006). A single angler seems to have little impact on a fish population compared to a commercial fishing operation, however this perspective overlooks the pressure millions of individual anglers can cause (Lewin et al. 2006). Hansen et al. (2005) indicated angling might not be as self-regulating (angler effort decreases as fish populations decline) as previously thought because the relationships between anglers catch rates and abundance is not linear (e.g., catch rates remain high even as fish density declines). Recent technologies have increased the effectiveness of anglers allowing them to find and exploit fish populations even when abundance is low (Post et al. 2002). Lack of long-term monitoring programs, management actions shielding the decline of fish populations (e.g., stocking) and the complexity of angler behavior make it difficult to define the impact of angling (Post et al. 2002).

Studies on the dynamics of unexploited fish population are rare in the fisheries literature (Hilborn and Walters 1992). When considering the economic value of fishing this is not surprising. In 2011, 27.5 million Americans fished 456 million days with expenditures for trips and equipment totaling $25.7 billion for the year (U.S. Fish and Wildlife Service 2011). With the increasing popularity of tourism to remote areas and the access provided by forestry roads (Kaufman et al. 2009), many fish populations that were previously unexploited or lightly fished are facing increased angling pressure. Therefore, unexploited fish populations are essential for comparative analyses of the long-term effects of exploitation, providing information to develop management strategies for exploited populations.

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Chapter 2: Population characteristics of a closed Northern Pike (*Esox lucius*) catch-and-release population in Minnesota

Abstract. - Literature regarding catch-and-release populations of Northern Pike are rare and provide a unique perspective on their population dynamics. Shingobee Lake is a 64-ha mesotrophic lake with a maximum depth of 12.2 m located in northern Minnesota. Northern Pike fishing has been catch-and-release only since 2005, and there are no public accesses on the lake. Annual ice-out trap-netting occurred from 2009-2017, and a sizable amount of the Northern Pike recaptured via trapnet or angling had been previously tagged (37-59%). The lack of exploitation and high tagging percentage provided a unique opportunity to study the population dynamics of Northern Pike. Shinogbee's population of Northern Pike is female dominated and consists of old, slow growing, large individuals. The overall capture ratio of female:male fish was 1.75:1. Only 2.1% of the sampled males were over 600 mm, compared to 37.2% of the female population. Abundance estimates throughout the study period remained stable (21 to 33 fish/ha) and a catch curve indicated an overall mortality rate of 31%. Female Northern Pike grew faster than males in Shingobee Lake, however both sexes lagged behind an international growth standard. Weisberg's mixed effect growth model showed little year-to-year (environmental) or cohort base variation in growth. Proportional size distribution ranged from 42-56, indicating a stable size structure throughout the study period. The results of this study support the argument that restricting harvest can improve the size structure of a Northern Pike population. Management aimed at improving pike size structure must take into account the importance of protecting large, older individuals.

INTRODUCTION

Northern Pike *Esox lucius* has been characterized as a mesothermal cool-water species that is best adapted for shallow, moderately productive, mesotrophic-eutrophic environments (Casselman 1978). Northern Pike are a keystone piscivore in cool-water habitats and can influence species composition, abundance and distribution of many species in a fish community (Craig 2008). The Northern Pike is the most widespread game fish in Minnesota and provides many recreational fishing opportunities in the state's lakes and rivers. They are found in all major drainages in Minnesota and have been sampled in 3,906 lakes by the Minnesota Department of Natural Resources (Pierce et al. 1995).

Growth of Northern Pike is generally fastest during their first year of life and progressively slows as the fish increases in age. Seasonally, growth of individual pike is most rapid when temperatures increase during the spring and early summer, then decreases through late summer and fall, and is relatively slow during the winter (Casselman 1996). Growth rates of individual Northern Pike are influenced by fish density and the environmental characteristics of the waters they inhabit. Jacobson (1992) found several factors were correlated with Northern Pike growth in Minnesota, the most significant being length of growing season (positive relation) and water transparency (negative relation). Although environmental factors affect fish growth and population size structure, Backiel and Le Cren (1978) observed that without knowledge of density and its effects on growth, environmental influences are of little value.

High density of Northern Pike in an ecosystem often stunts or slows their growth, resulting in size structures undesirable to anglers. Diana (1987) describes stunting as a reduction in juvenile growth and a near cessation of growth in adulthood. Stunting results from factors such as exploitation of large Northern Pike (Pierce et al. 1995), lack of appropriate prey items, and lack of thermal refuges (Diana 1987) and is typically associated with high population density (Casselman 1978, Diana 1987). Northern Pike may be more prone to stunting in smaller lakes. A study by Goeman et al. (1993) showed that high-density, slow-growing Northern Pike populations were common in Minnesota lakes less than 200 ha in area. Stunted populations of Northern Pike present a significant management problem. Attempts to restore a healthier population balance are being made through the application of protected slot limits, minimum length limits or through the encouragement of catch-and-release fishing (Paukert et al. 2001). A study in north-western Wisconsin transferred Northern Pike from a high-density population to a low-density population to see if condition and growth improved. Transferred fish showed improved growth and condition, due to less competition between fish and an increased abundance of larger prey items (Margenau 1995). Goeman and Spencer (1992) found removal of Northern Pike by intensive trap-netting to be ineffective in altering population size structure. After 6 years of trap-netting, no changes in abundance, growth or population size structure were documented.

A significant proportion of the Northern Pike population dies each year from natural causes and fishing mortality. Total mortality rates include both natural causes and fishing mortality. Margenau et al. (1998) found the total annual mortality rates for Northern Pike in 17 northern Wisconsin lakes to range from 35% to 79%. Pierce and Tomcko (2003) found annual mortality rates for seven north-central Minnesota lakes to range from 36% to 63%. A mark-recapture study by Pierce et al. (1995) showed that recreational fishing caught 4% to 22% of Northern Pike ≥ 350 mm) that had been tagged, averaging an annual exploitation rate of 10%. Total annual mortality for fish ≥ 350 mm was estimated at 48%, demonstrating the important role of natural mortality in Northern Pike population dynamics.

Recreational angling in Minnesota is highly selective for large Northern Pike (> 600 mm), even though fish as small as 350 mm can be caught (Cook and Younk 1998). A result of this size selectivity, coupled with historical increases in fishing effort, is that size structures of Northern Pike in Minnesota have declined and fewer trophy-sized fish are present. A long-term evaluation of length limit regulations for Northern Pike in 22 Minnesota lakes by Pierce (2010) found on a broad scale an improvement in the size structure but no consistent trends in relative abundance when compared to reference lakes. The study also stressed the importance of long time periods needed to evaluate regulations, which can be difficult due to the fishing public expecting immediate results.

Shingobee Lake presents a unique perspective on the size structure of Northern Pike in Minnesota, due to light fishing pressure for most of the twentieth century, no public access, and catch-and-release only Northern Pike fishing since 2005 (D. C. Hudson, United States Geological Service, personal communication). Literature regarding unexploited Northern Pike populations is rare (Mosindy et al. 1987), therefore, Shingobee Lake will offer a unique perspective on the population dynamics of a catch-and-release Northern Pike population. Gaining knowledge on pike size structure over a long period of time will provide useful information regarding how density, growth, abundance and mortality affect fish populations. The main objectives of this study are to

1) describe the population dynamics of Northern Pike in a catch-and-release fishery and 2) compare these parameters to exploited populations.

METHODS

Study Site

Shingobee Lake is a 64 ha lake located on private property in Hubbard County (47°0′N, 94°41′W) with 17 ha of littoral zone and a maximum depth of 12.2 m. The entire shoreline is natural and heavily vegetated with stands of water lilies *Nymphaea* spp., bulrushes *Schoenoplectus* spp. and wild rice *Zizania palustris*. The lake bottom consists mainly of silt, marl and sand (Locke and Schwalb 1997). There are no public accesses; however, there is a United States Geological Survey field station located on the lake supported by the Shingobee Headwaters Aquatic Ecosystems Project (Winter 1997).

Sampling

Trap nets were fished to sample Northern Pike every spring during 2009 through 2017. The nets were set directly after ice-out while the fish were staging for spawning and fished daily until reduced catches indicated spawning was near completion. The trap nets are 1.2 m x 1.8 m with a 12 m lead and a 25 mm bar mesh. Trap nets were set perpendicular to shore for a period of 24 hours before being pulled. No attempt was made to randomize trap-net effort; effort was directed at sampling the greatest number of fish possible. Captured fish had their total length and sex (when possible) recorded. Because determination of sex using external characteristics was found to be unreliable, sex was recorded only for Northern Pike extruding sexual products (Casselman 1974). Numbered t-bar achor tags (25-mm monofilament, yellow) were inserted lateral to the dorsal fin into untagged Northern Pike following the methods of Pierce and Tomcko (1993), and the tag number was then recorded (if previously tagged, that number was recorded). A scale sample was taken from the preferred zone adjacent to, but not on, the lateral line above the pelvic fins as described by Williams (1955). Scales were placed in individual coin envelopes marked with the tag number, date, sex, and length of the fish.

Northern Pike caught by hook and line year-round throughout the study had similar data collection methods as trap nets. Numbered t-bar anchor tags were inserted into untagged fish (or the number was recorded if a tag was present), the date was recorded, and the fish was measured and then released back into the lake.

Scale aging

Scale aging was accomplished following the methods of Schneider (2001). All Northern Pike sampled during the spring spawning season were aged. Pike recaptured in trap nets that were previously aged were not aged again due to a decrease in aging accuracy with increasing fish age (Casselman 1996, Rude et al. 2017). There was one scale reader for the first six years of the study (2009-2015), after this time period a new reader took over. One hundred previously aged fish were subsampled by 75 mm length groups and aged by the new reader. The average coefficient of variation (ACV) between the two readers was 3.7%, falling within the recommended guidelines by Campana (2001) of an ACV value of less than 5%.

Population Dynamics

Abundance

The Jolly-Seber model (Jolly 1965, Seber 1965) was used for estimating the abundance of Northern Pike. The Jolly-Seber method was applied because the study spanned multiple years and had an indefinite time in between sampling events (angling).

Each individual year of the study was treated as a single marking event, and the following years were the resampling events. All Northern Pike captured by trap-netting or angling > 350 mm were included in the estimates, and if a fish was captured more than once in a year, only the first capture event was used. The assumptions necessary for accurate estimation of abundance with the Jolly-Seber model are as follows:

1) every fish in the population has the same probability of capture in the *i*th sample;

2) every marked fish has the same probability of surviving from the *i*th to the (*i*+1) sample and being in the population at the time of the $i + 1$ sample;

3) marked fish do not lose their marks between sampling events (Pierce and Tomcko 1993 reported 1.8% annual tag loss) and all marks are reported on recovery; and,

4) all samples are instantaneous (sampling time is negligible).

Survival/Mortality

Annual apparent survival (φ) estimates were calculated using the Jolly-Seber method (Jolly 1965, Seber 1965). Apparent survival is the product of the probabilities of true survival and of study area fidelity (Schaub and Royle 2014). Apparent survival was used due to the population being open and without information (e.g., telemetry data) to distinguish between mortality and emigration. The assumptions for estimating survival using the Jolly-Seber method are noted in the previous abundance section. Total mortality for Northern Pike of each sex was estimated from a catch curve (Ricker 1975).

Growth

Growth of Northern Pike was determined by fitting the von Bertalanffy (von Bertalanffy 1938) growth equation to length at age for each sex:

$$E[L|t]=L\infty(1-e^{-K(t-t0)})$$

where:

- $E[L|t]$ is the expected or average length at time (or age) t
- $L\infty$ is the asymptotic average length
- K is the so-called Brody growth rate coefficient, and
- $t0$ is a modeling artifact and not a biological parameter

A mixed effects linear growth model developed by Weisberg et al. (2010) was used to explain yearly growth of Northern Pike. All fish that were captured in back-to-back years (i.e. 2009-10, 2010-11) and had been assigned an age and sex were included in the models. Males and females were modeled separately due to their differences in maximum length and maximum age. Literature shows male pike typically grow at a lesser rate and achieve a smaller maximum size when compared to females (Casselman 1996; Margenau et al.1998; Pierce et al. 2003; Pierce and Tomcko 2003). Variables included in the analysis were age, recapture year, birth year, months between capture and tag ID number. A minimum number of entries (N = 5) for each variable were sought (except tag ID). Age, recapture year, birth year, and months between capture were treated as fixed variables and tag ID was treated as a random variable. Tag ID is treated as a random variable due to fish specific-growth effects (i.e. fast or slow growing fish). Any fish exhibiting negative growth between recapture events (likely due to small measurement errors) were assumed to not have changed in length (Rude et al. 2017). Growth measurements were log(y + 1) transformed to ensure no pattern was evident in the residual plot while allowing a growth of “0” to be included in the models. The models selected to explain growth can be found in Table 3. Akaike’s information criterion (AIC) was used to select the best-supported model for growth for each sex (Akaike 1998). The model with the lowest AIC was selected as the best-supported model, though models with Δ AIC < 2 were also considered (Anderson et al. 2000). In the event two models had a Δ AIC < 2, the simpler of the models was selected as the best supported.

Proportional Stock Density (PSD)

Proportional stock density (the proportion of fish ≥ 350 mm that were also ≥ 530 mm) was calculated and used as an index of Northern Pike population size structure, following the size categories proposed by Gabelhouse (1984). Preferred (PSD-P) (the proportion of fish ≥ 350 mm that were also ≥ 710 mm) and memorable (PSD-M) (the proportion of fish ≥ 350 mm that were also ≥ 860 mm) PSD indexes were also calculated.

Pooled Minnesota Lake Data

Density, back-calculated mean length at age, and PSD data were obtained from 9 of 12 Minnesota lakes (27-180 ha) studied by Pierce et al. (2003). These lakes are the best representation of similar systems to Shingobee Lake in size and geographic location found in the literature. Lake characteristics and population dynamics can be found in Tables 6 and 7. Shingobee Lake was also compared to the relationship of littoral area and PSD/density in Northern Pike found by Pierce and Tomcko (2005). All analyses were performed in Program R (R Core Team 2016).

RESULTS

Abundance

The number of individual Northern Pike captured on an annual basis by trap-netting and angling ranged from 555 to 1,305 unique individuals from 2009-2017. The percentage of individuals previously tagged ranged from 37-59% (Table 1). Jolly-Seber population estimates ranged from 1,354 to 2,120 in Shingobee Lake with density estimates ranging from 21 to 33 fish/ha with a mean of 26 fish/ha (95% CI, 21-30) from 2010-2016 (Figure 1).

The sampled ages of male and female Northern Pike were 2 to 11 and 2 to 16, respectively. Few male fish were older than 7 (5.4%) while a sizable proportion of females reached this age (26.2%) (Figure 2). Females were predominant in older age groups. The ratio of males and females sampled varied by capture method. Trap-netting captured more females than males (1.28:1), and females were angled over double the rate of males (2.60:1) for an overall capture ratio of 1.75:1 females to males. This ratio fluctuated slightly but stayed close to the same throughout the study (Figure 3).

Survival/Mortality

Annual apparent survival (φ) estimated via mark-recapture (Jolly-Seber method) ranged from 0.51-0.78 in Shingobee Lake from 2009-2015 with a mean of 0.69 (95% CI, 0.58-0.80; Figure 1). A catch curve estimated total mortality throughout the study at 0.42 (95% CI, 0.40-0.44) for males and 0.30 for females (95% CI, 0.28-0.31; Figure 4). Combined mortality for males and females throughout the study was 0.31 (95% CI, 0.30-0.32). Apparent survival fluctuated slightly (Figure 1), however, the mean throughout the study period (0.69) was extremely similar to catch curve estimates. Overall mortality estimated via catch curve, had a survival rate of 0.69 throughout the study.

Growth/PSD

The longest male captured was 782 mm, however, only 2.1% of the sampled males were over 600 mm. The longest female captured was 1,003 mm, with 37.2% of the sampled females over 600 mm. Modeling of growth with the von Bertalanffy equation by sex yielded values of 573 and 1170 mm for $L\infty$, K values of 0.302 and 0.075 and $t0$ values of -1.943 and -3.894 for males and females, respectively (Figures 5, 6). Growth of female pike was greater when compared to males in Shingobee Lake (Figure 8). Growth of males in Shingobee Lake was similar at ages 2, 3 and 4 when compared to exploited pike populations studied by Pierce et al. (2003), but slowed at age 5 (Figure 7). Mean length at age 5 for males was 492 mm (95 % CI, 488-496 mm) in Shingobee Lake and mean backcalculated length at age 5 was 544 mm (95% CI, 497-592 mm) in exploited MN lakes studied by Pierce et al. (2003). Growth of females in Shingobee Lake was similar at ages 2 and 3 when compared to exploited pike populations studied by Pierce et al. (2003), but slowed at ages 4 and 5 (Figure 7). Mean length at age 5 for females was 544 mm (95% CI, 539-551 mm) in Shingobee Lake and mean backcalculated length at age 5 was 610 mm (95% CI, 565-655 mm) in exploited MN lakes studied by Pierce et al. (2003). Growth of males and females lagged behind the international growth standard (undifferentiated by sex) by Casselman (1996) after they reached a certain age. Male and female growth was similar to the international growth standard up until it slowed at age 4 and age 5 Casselman 1996; Figure 8). However, female growth was comparable to the growth standard again after reaching age 9.

Weisberg’s mixed effect growth model indicated very little year-to-year (or environmentally caused) growth rates of Northern Pike in Shingobee Lake. The best-supported model for both males and females included the variables age (Table 4) and months between capture (Table 5). Male pike grew fastest until age 5, and then stayed uniform (Figure 9). Female pike grew fastest until age 5, and then growth slowed and was nearly uniform from ages 6 to 12 before declining once again (Figure 9). Months between capture was included in the best model and the longer the interval in between captures, the greater the growth of the fish (Figure 10). Recapture year and birth year were not included in the best model; therefore, most of the meaningful variation in growth for both sexes was due to the age of the fish and the interval between captures.

Proportional size distribution of Northern Pike in Shingobee Lake varied from 42 (95% CI, 27-47) to 56 (95% CI, 51-62) between 2009-2017 with a mean PSD of 51. PSD-P and PSD-M ranged from 9 (95% CI, 6-11) to 23 (95% CI, 17-18) and 2 (95% CI, 1-4) to 6 (95% CI, 2-8), respectively (Figure 11).

Littoral Area vs PSD/Density

Pierce and Tomcko (2005) found a significant relationship between littoral area of a lake and density of Northern Pike/ha. After excluding larger lakes from their data set (as previously described), a regression analyses showed percent littoral area as the best predictor for explaining differences in density ($R^2 = 0.95$, df = 7, $P < 0.0001$). Including the mean density of Northern Pike from Shingobee Lake throughout the study reduced the predictive ability of the regression model ($R^2 = 0.81$, df = 8, $P < 0.001$), with Shingobee Lake falling outside of the predicted range (Figure 12).

PSD has been related to percent littoral area in Northern Pike populations. In the nine exploited lakes studied by Pierce and Tomcko (2005), percent littoral area was a good predictor for PSD ($R^2 = 0.69$, df = 7, $P < 0.01$). Adding mean PSD through time on

Shingobee Lake to the regression model decreased the significance of the relationship ($R^2 = 0.58$, df = 8, $P < 0.05$), however it still fell within the prediction intervals (Figure 12).

DISCUSSION

Shingobee Lake provides a unique perspective on Northern Pike populations, with literature being rare on unexploited populations. In addition, few Northern Pike studies have spanned over a time period as long as our current study (8 years) or marked as high a percentage of the population (Range = 37-59%, Table 1). The Northern Pike population in Shingobee Lake can be described as a moderate density population with slow growth rates, high survival rates and older individuals when compared to other reported values for exploited lakes.

High densities of slow-growing fish are common among exploited Northern Pike populations (Pierce and Tomcko 2005). This commonly results in high mortality rates causing a stock piling of younger individuals, leading to a size structure undesirable to anglers. In the absence of fishing mortality, the combined forces of slow growth and low but steady natural mortality could potentially increase the abundance of older, larger fish. Shingobee Lake exhibits slow growth rates and moderate density, however, due to the lack of exploitation, it has a size structure comprised of older individuals compared to exploited populations.

Estimates of total annual mortality rates for Northern Pike have varied widely in the literature. High total annual mortality rates were reported from Escanaba Lake, Wisconsin ($A = 0.59$-0.91; Kempinger and Carline 1978), and low rates were reported by Mosindy et al. (1987) for a small, remote unexploited Ontario lake ($A = 0.19$). Other reported estimates from Wisconsin and Minnesota have ranged from $A = 0.35$-0.79

(Pierce et al. 1995; Margenau et al. 1998; Pierce and Tomcko 2003). A long-term study of Northern Pike mortality in Lake Windermere, England, found *A* varied from 0.56-0.59 (Kipling and Frost 1970). Shingobee Lake catch-curve estimates indicated a total annual mortality for females of 0.30 and 0.42 for males, and a combined mortality of 0.31, demonstrating how older, large females drive mortality rates in unexploited systems. Low mortality rates have allowed a stockpiling of larger, older individuals, which is uncommon in exploited systems (Pierce and Tomcko 1995, Pierce et al. 2003).

Recreational fishing at Shingobee Lake is catch and release only; therefore, natural mortality plays a critical role in Northern Pike population dynamics within this system. Small Northern Pike typically have higher mortality rates than large Northern Pike (Mosindy et al. 1987), and cannibalism may be an important source of natural mortality. Pierce et al. (1995) found Northern Pike second to only Yellow Perch *Perca flavescens* in the frequency of occurrence in stomachs of 129 Northern Pike sampled from two lakes. Mann (1982) and Grimm (1983) suggested that cannibalism accounted for most of the natural mortality in the River Fromme and experimental waters in the Netherlands respectively. Cannibalism by older Northern Pike in Shingobee Lake likely helps reduce the abundance of smaller individuals and thus helps to regulate the density of pike.

Growth of Northern Pike in Shingobee Lake was below the average compared to Minnesota lakes (Pierce et al. 2003, Figure 7) and the international growth standard (Casselman 1996, Figure 8). Mosindy et al. (1987) found growth rates of an unexploited Northern Pike population in Ontario to be below average compared to exploited waters in Ontario and Minnesota. In the absence of fishing mortality the combined forces of slow growth and low mortality seemed to increase the number of older, larger fish. An increased number of larger individuals in the lake likely caused an increase in food competition, which limited the growth potential of Northern Pike in Shingobee Lake. Shingobee Lake showed little variation in year-to-year growth, as indicated by the mixed effect linear model (Table 3). Shingobee Lake does not have a significant amount of littoral area (26%), therefore, water temperature (year-to-year variation) was not a significant factor relating to Northern Pike growth. The growth modeling illustrated inter-annual weather changes did not have a big effect on growth rates. Available habitat and fish density play a large role in determining Northern Pike growth rates in Shingobee Lake and both of these factors have remained stable through time.

The size structure and estimated abundance of Northern Pike in Shingobee Lake has been stable throughout the study period. After 2009, the first year of the study, proportional stock density increased from 42 to 48, and then stayed in between 48-56 from 2010-17. The largest annual change in abundance estimates was 509, and from 2013-2016 population estimates were within ± 250 individuals (Figure 1). Margenau et al. (1998) studied Northern Pike populations in 19 small (<120 ha) northern Wisconsin lakes and found a wide range of PSD (3-90) and most populations (68%) had truncated size structures with less than 25% of the adult Northern Pike larger than 530 mm. Shingobee Lake had at least 39% of the adult Northern Pike population over 530 mm with an average of 48% (95% CI 44-54%) from 2009-2017. The high percentage of larger individuals found in Shingobee Lake is likely caused by low mortality rates due to no angler harvest.

Previous studies have shown percent littoral area as the most important variable explaining differences in Northern Pike densities. Pierce and Tomcko (2005) found littoral area to be the best predictor of Northern Pike densities in 16 north-central Minnesota lakes using a regression analyses ($R^2 = 0.88$). They found extensive proportions of littoral area to support higher densities of Northern Pike, but smaller average sizes. Shingobee Lake has a higher density of Northern Pike than would be expected with the percentage of littoral area in the lake (Figure 12). Shingobee Lake's density of Northern Pike is likely inflated due to the lack of exploitation allowing the stockpiling of larger individuals.

Female Northern Pike are more abundant in Shingobee Lake compared to other systems. Casselman (1975) looked at Northern Pike sex ratios for 4,802 individuals captured via nets, electrofishing and angling from three Ontario populations. Females were captured more often angling (1.24:1) and by nets and electrofishing (1:14:1). Margenau et al. (1998) found the ratio of females to males captured by trap nets during the spring spawning run in 19 small (<120 ha) northern Wisconsin lakes to be 1:1.5. The MNDNR extensively netted a small bog lake and removed almost half of the estimated population of age-2 and older Northern Pike. Fish achieved a maximum age of 7, and males were predominant in older age groups, however, each sex contributed 50% to the whole population (1:1). Shingobee Lake females were captured more frequently angling (2.60:1) and by trap net (1.28:1) than males throughout the study (Figure 3). Combined, the female to male ratio was 1.75:1. This follows a similar pattern as reported by other studies, that during the spring spawning run males and females are captured around the same rate. Studies involving angling and sex ratios commonly report a higher capture of females to males. Casselman (1975) and Johnson (1969) found sex ratios of 1.24 and 1.22 females to males angled from the St. Lawrence River and the Murphy flowage, respectively. Shingobee Lake is closed to harvest, which may explain why females are captured at a much higher rate. In exploited systems, the larger, faster-growing individuals are usually females, and fishermen have been shown to be size-selective. Pierce et al. (1995) found annual exploitation rates for larger Northern Pike (> 500 mm total length) to be 2 to 9 times higher than for smaller fish (≥ 500 mm). Northern Pike can be highly vulnerable to angling (Weithman and Anderson 1978, Beyerle 1978) and fishing effort can remove a large portion of pike populations.

MANAGEMENT IMPLICATIONS

The results of this study support the argument that restricting harvest (using catch and release only) can improve the size structure of a Northern Pike population. Before harvest of Northern Pike stopped in 2005, the lake had a high abundance of smaller pike and few large pike were observed (D. C. Hudson, United States Geological Service, personal communication). Shortly after harvest ceased, the size structure for Northern Pike shifted to include larger, older fish. In Shingobee Lake, it was possible to improve the size structure of fish, likely due to a lack of exploitation. Other studies have attempted to improve size structure with mixed results. Margenau (1995) transferred Northern Pike in Wisconsin from a high-density population to a low-density population and noticed improved growth and condition, attributing it to less competition and an increased abundance of larger prey items. Goeman (1993) tried to improve Northern Pike size structure in a Minnesota lake by intensive trap-netting by reducing the density of fish. After 6 years of trap-netting, no changes in abundance, growth or size structure were documented. Pierce (2010) looked at the effects of maximum, minimum, and slot length limits on the sizes and relative abundance of Northern Pike in 22 Minnesota lakes. The regulations did not achieve the desired management objectives in every lake, but on a broader-scale, the statewide finding showed an improved size structure but no significant trends in relative abundance.

Catch and release fishing may not always improve size structure and Shingobee Lake has a couple of advantages other systems may not. Property around the lake is owned by only three individuals and there is no public access, leaving fishing pressure to a minimum. Shingobee Lake has a population of Cisco *Coregonus artedii* and a maximum depth of 12.2 m, allowing a thermal refuge for large Northern Pike during the warm summer months. Data spanning 65 years from a fishing contest in northern Minnesota showed most large Northern Pike came from systems with deep water and supported a population of Cisco (Jacobson 1992). Many smaller lakes in Minnesota may not meet these requirements; however, where these conditions exist it’s reasonable to assume Northern Pike size structure could be improved by protecting older, larger fish.

Our study of Shingobee Lake found an unexploited population of Northern Pike to be female dominated and consist of old, slow growing, large individuals. While it is uncommon for these conditions to exist, Shingobee Lake demonstrated Northern Pike size structure can potentially be shifted to include larger individuals as a result of catch and release angling. Fish density and available habitat were more important factors influencing Northern Pike growth when compared to year-to-year changes in weather patterns. This study suggests not harvesting large Northern Pike can improve size structure on a smaller northern Minnesota lake. These principals could be applied to the management of similar systems in which large Northern Pike are absent.

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Table 1. Number of unique fish captured in Shingobee Lake from 2009-2017.

	Capture Year								
Method	2009	2010	2011	2012	2013	2014	2015	2016	2017
Angling	639	719	783	664	686	613	469	294	474
Trap net	141	145	371	641	152	183	168	261	229
Tagged (%)	-	38	44	51	54	59	55	51	37
Total	780	864	1154	1305	838	796	637	555	703

Table 2. Age-frequency distributions of Northern Pike caught by trap-netting and angling in Shingobee Lake from 2009-2017. Note: all fish that were sexed during trap-netting were aged and then assigned a sex for the next capture (fish were unable to be sexed caught via angling).

	Trap net			Angling		
Age	Males	Females	Unknown	Males	Females	Unknown
1	0	1	1	8	9	50
2	102	58	11	67	89	214
3	142	100	9	90	142	154
4	178	163	4	100	189	111
5	155	168	4	96	199	86
6	101	139	9	80	170	53
7	52	94	3	44	141	40
8	18	75	2	16	105	22
9	15	57	1	10	83	21
10	7	46	1	3	51	12
11	1	38	0	0	26	6
12	0	25	0	0	27	4
13	0	14	0	0	14	1
14	0	5	0	0	12	2
15	0	3	0	0	5	0
16	0	1	0	0	2	0
Sum	771	987	45	514	1264	776

Table 3. Results from mixed model analysis for the five candidate models for Northern Pike growth, parentheses represent variables treated as random interactions. Models are ordered from top to bottom from the lowest to highest Akaike's information criterion (AIC), thus the first candidate model listed is the best supported. Tested variables were Age, Recapture Year (R. Year), Birth Year (B. Year), Months Between Capture (M. B. Cap), and Tag ID.

	Males		Females	
Model	AIC	Δ AIC	AIC	Δ AIC
Growth ~ Age + M. B. Cap + (Tag ID)	1326.5	0.0	3137.3	0.0
Growth ~ Age + R. Year + M. B. Cap + (Tag ID)	1328.7	2.2	3145.2	8.0
Growth ~ Age + B. Year + M. B. Cap + (Tag ID)	1338.7	12.2	3174.0	36.7
Growth ~ Age + R. Year + B. Year + M. B. Cap + (Tag ID)	1346.2	19.7	3181.3	44.0
Growth ~ Age + (Tag ID)	1347.2	20.7	3269.1	131.8

Table 4. Northern Pike age distribution by sex in Shingobee Lake used in the mixed model analysis.

Age	3	4	5	6	7	8	9	10	11	12	13	14	15
Males	65	90	95	81	48	19	8	7	-	-	-	-	-
Females	69	122	166	167	119	100	76	52	39	26	21	8	8
Total	134	212	261	248	167	119	84	59	40	26	21	8	8

Table 5. Months between capture of Northern Pike by sex in Shingobee Lake used in the mixed model analysis.

M. B. Cap	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Males	5	2	6	22	23	38	49	53	74	41	30	36	18	10	3	2	2
Females	15	13	38	48	67	107	99	110	153	64	82	78	37	39	14	12	10
Total	20	15	44	70	90	145	148	163	227	95	112	114	55	49	17	14	12

Table 6. Lake characteristics and selected population dynamics from 9 north-central Minnesota lakes (Pierce et al. 2003).

Lake	Surface area (ha)	Littoral Area (%)	Year Sampled	Density (fish/ha)	Trap net PSD[a] (%)
Medicine	180	68.6	1993	36.5	26
North Twin	127	41.9	1993	13.8	45
Sissabagamah	148	60.1	1994	24.4	15
Wilkins	151	28.5	1994	11.9	48
Lake-of-Isles	25	77.5	1995	35.7	17
Willow	96	22.7	1996	3.2	55
Forest	15	40.8	1997	9.2	57
Sand	48	63.2	1998	26.3	29
Camerton	28	100.0	1998	59.0	22

[a] Proportional stock density

Table 7. Mean back calculated lengths at ages 2-5 for male (M) and female (F) Northern Pike from 9 north-central Minnesota lakes (Pierce et al. 2003).

		Mean back-calculated length (mm)			
Lake	Sex	Age 2	Age 3	Age 4	Age 5
Medicine	F	436	533	577	631
	M	396	455	491	533
North Twin	F	345	459	538	601
	M	300	398	453	505
Sissabagamah	F	340	440	506	558
	M	313	409	447	469
Wilkins	F	444	541	596	651
	M	409	497	548	597
Lake-of-Isles	F	383	432	500	514
	M	348	426	479	501
Willow	F	486	565	638	684
	M	466	542	589	621
Forest	F	426	535	622	689
	M	421	514	600	644
Sand	F	299	420	503	586
	M	274	382	452	498
Camerton	F	368	460	540	577
	M	361	440	496	532

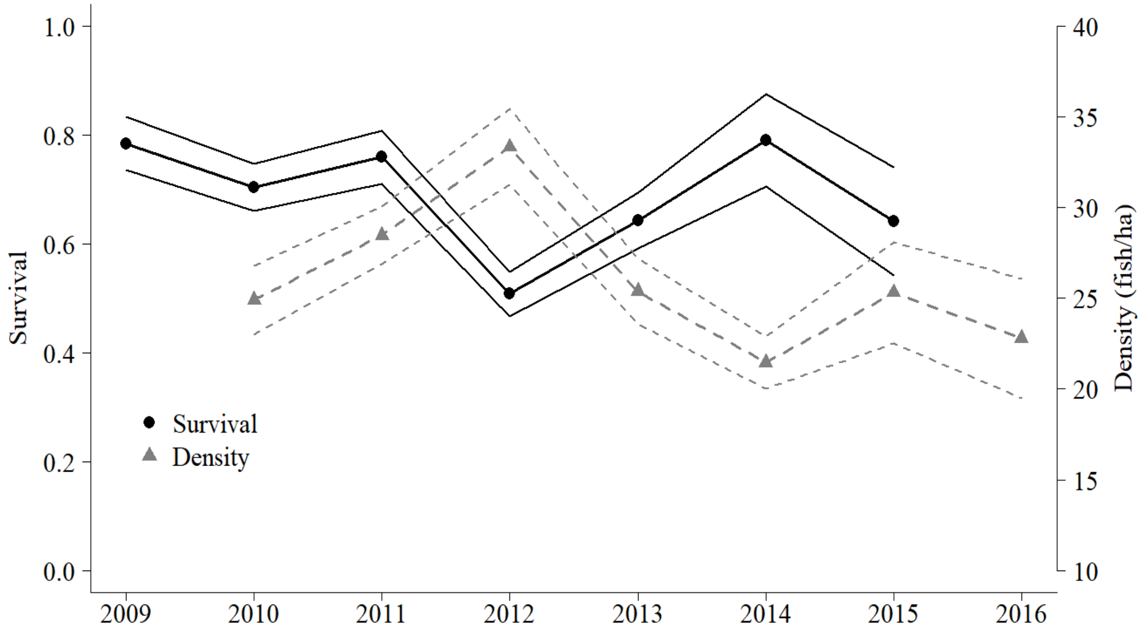

Figure 1. Jolly-Seber density and apparent survival estimates of Northern Pike in Shingobee Lake from 2009-2016. Dashed lines represent 95% CI.

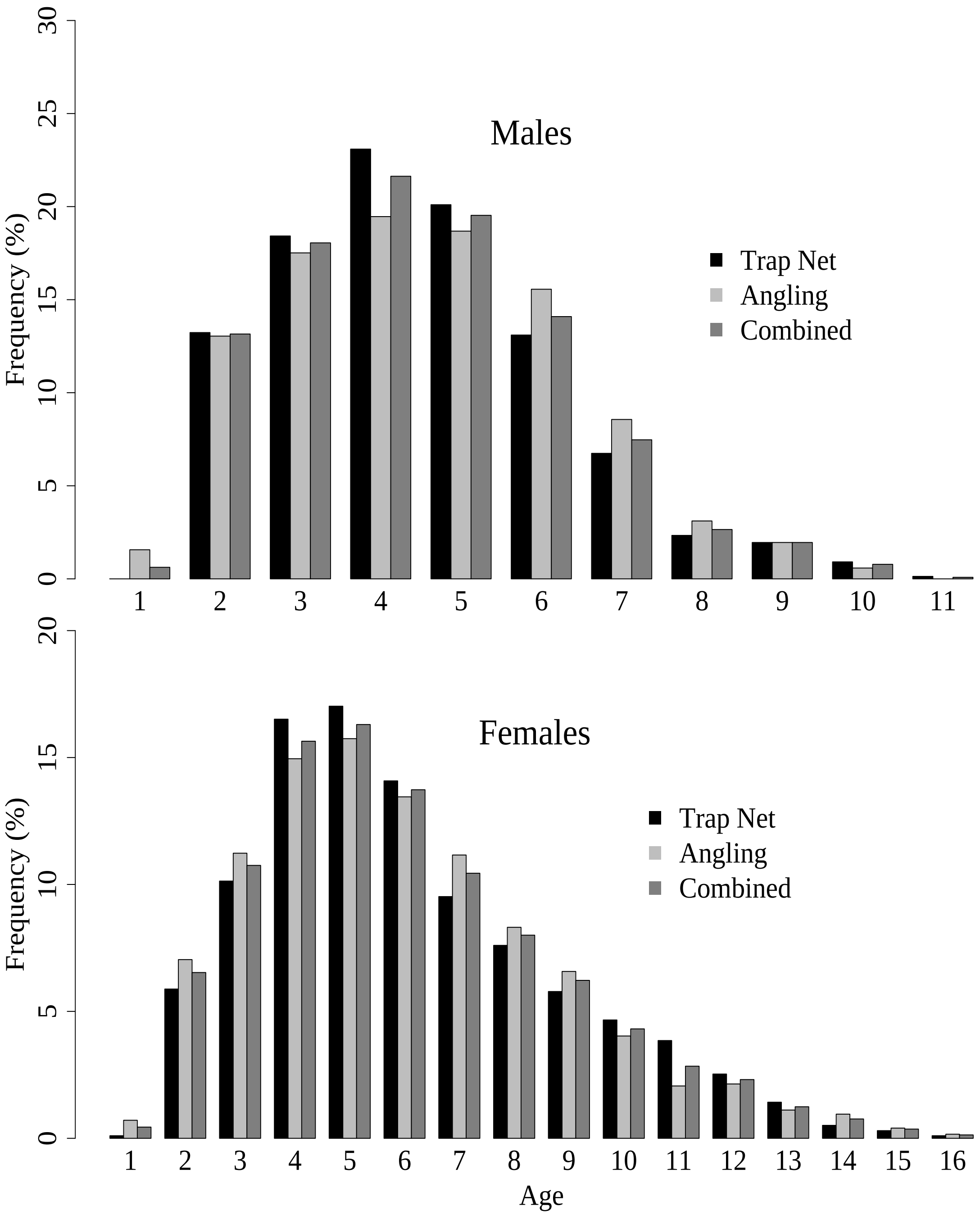

Figure 2. Age distributions of male and female Northern Pike sampled in Shingobee Lake from 2009-2017.

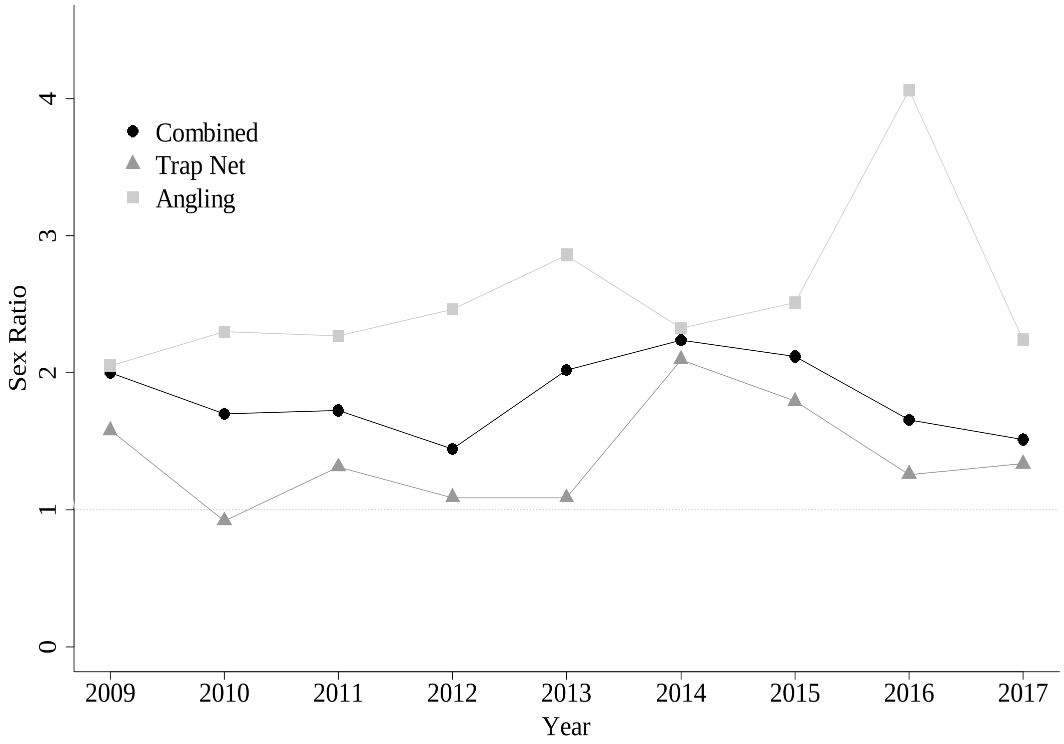

Figure 3. Sex ratio of female:male Northern Pike in Shingobee Lake from 2009-2017. The dotted grey line represents a sex ratio of 1:1.

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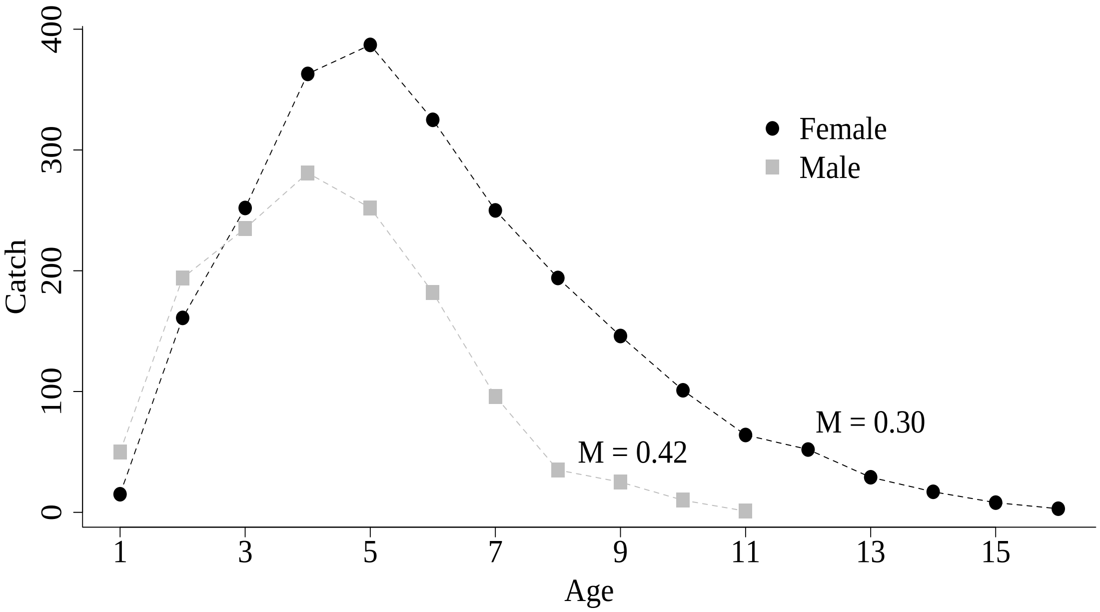

Figure 4. Catch-curve mortality estimates of female and male Northern Pike from 2009-2017 in Shingobee Lake.

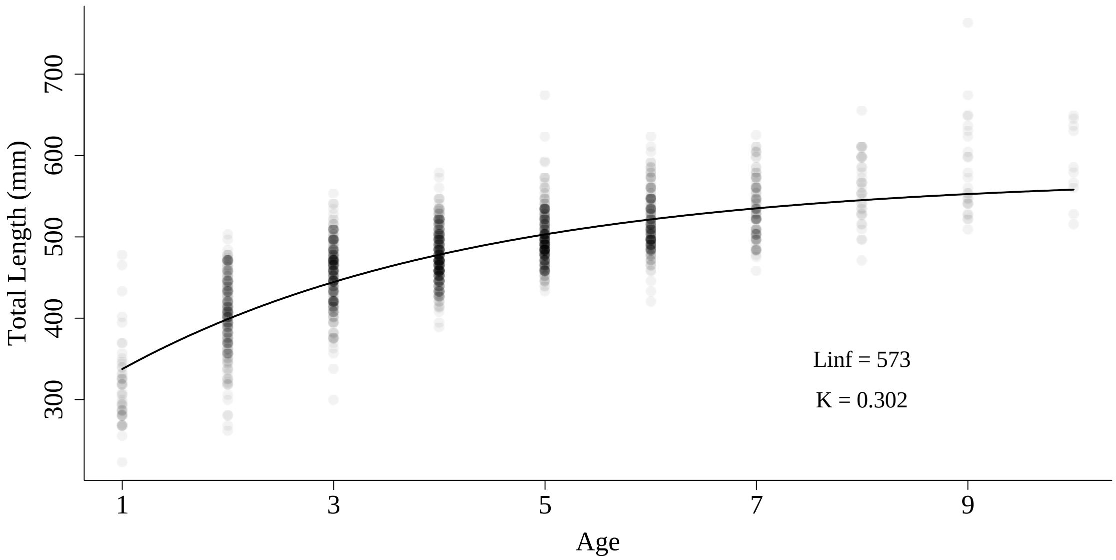

Figure 5. Length at age of male Northern Pike in Shingobee Lake fit to the von Bertalannfy growth model.

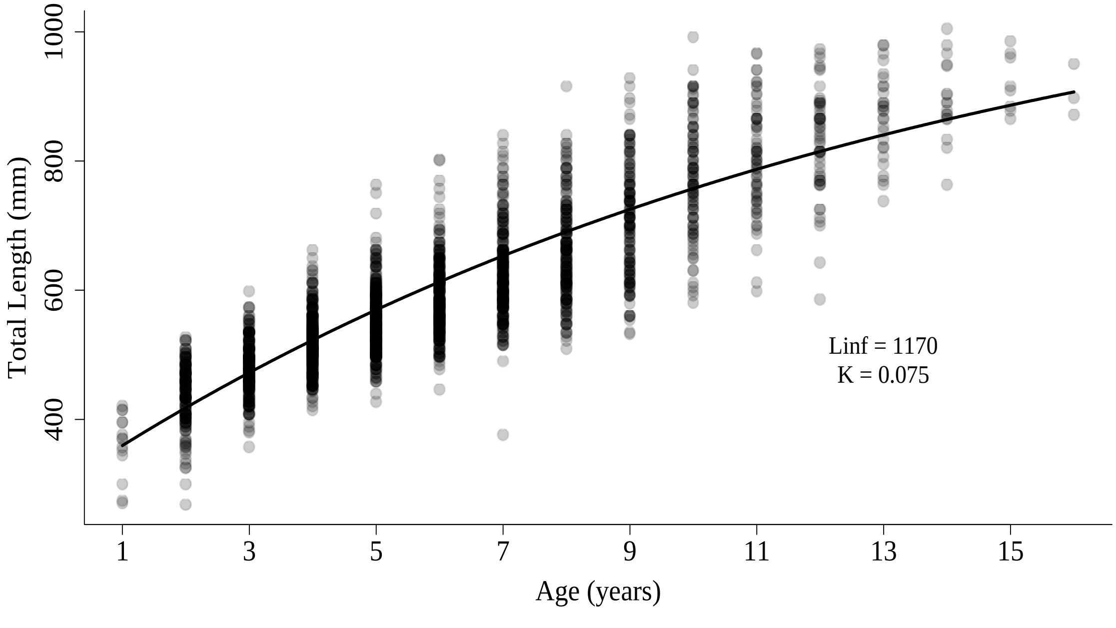

Figure 6. Length at age of female Northern Pike in Shingobee Lake fit to the von Bertalannfy growth model.

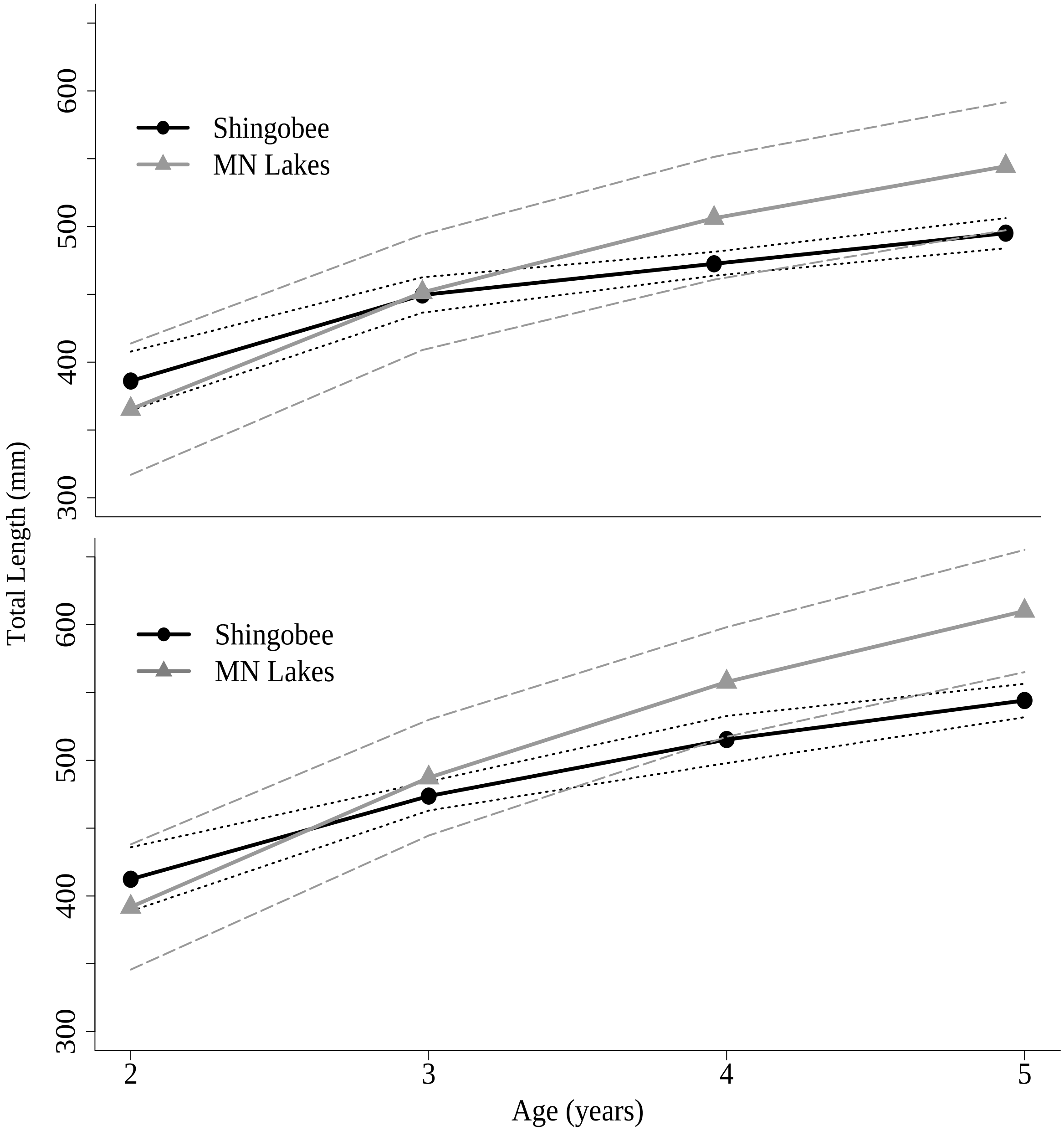

Figure 7. Mean length at age of male (top) and female (bottom) Northern Pike from Shingobee Lake compared to mean back-calculated length at age for pooled MN lakes (Pierce et al. 2003). Dashed lines represent 95% confidence intervals.

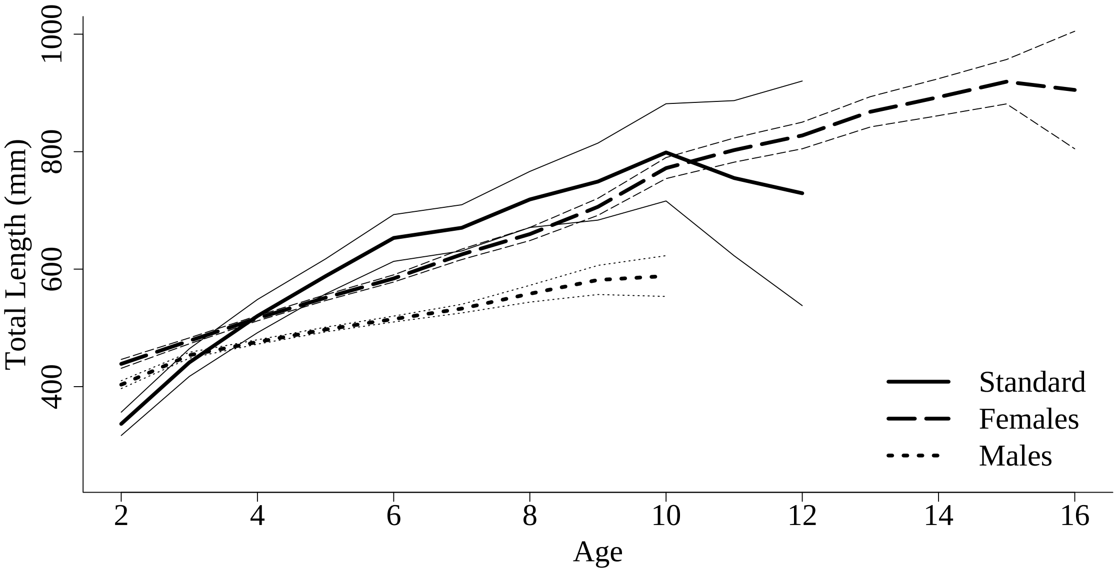

Figure 8. Mean total length at age of male and female Northern Pike from 2009-2017 in Shingobee Lake, and comparisons with upper and lower 95% confidence limits of an international growth standard for Northern Pike (Casselman 1996).

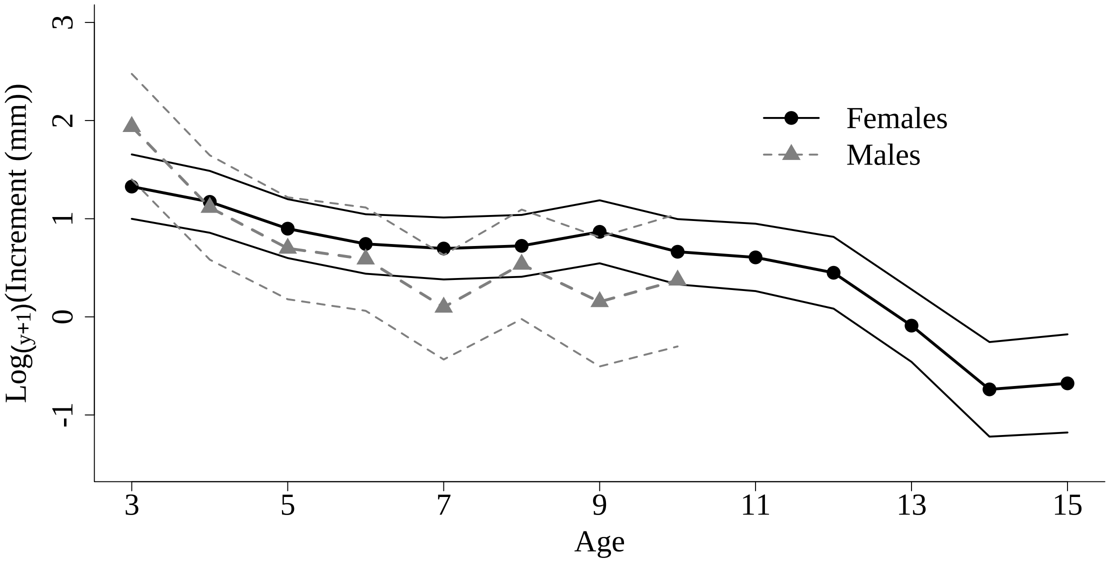

Figure 9. Growth coefficients (± SE) describing the age effects on growth of Northern Pike using the mixed effect linear growth model.

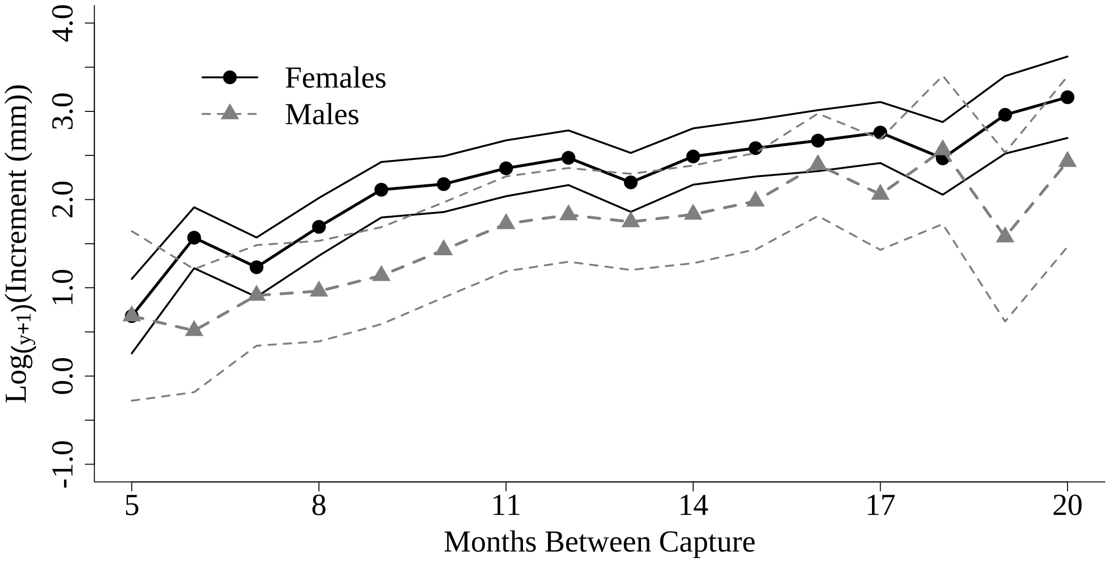

Figure 10. Growth coefficients (± SE) describing how months between capture effect growth of Northern Pike using the mixed effect linear growth model.

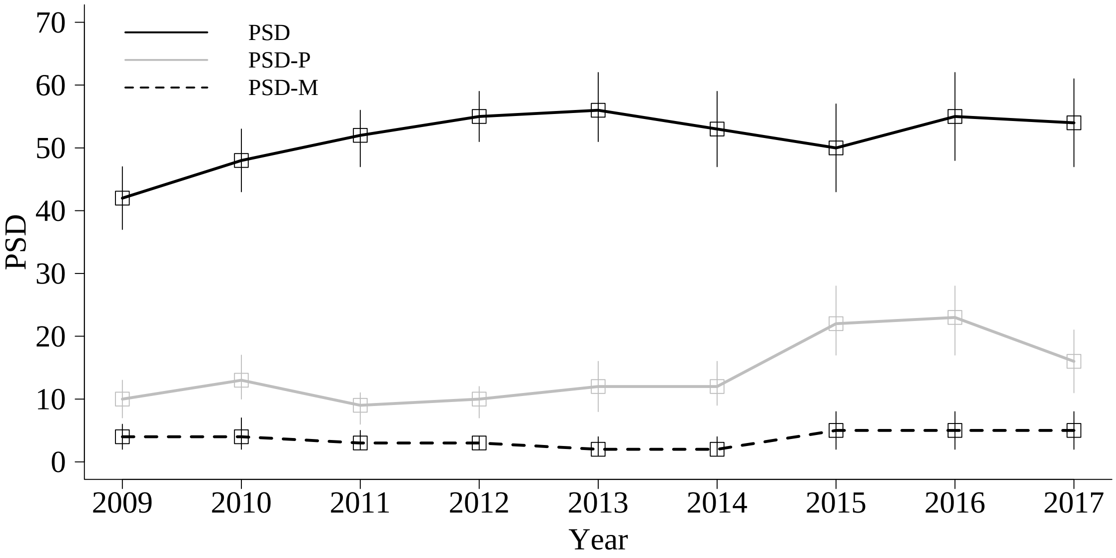

Figure 11. PSD, PSD-P, and PSD-M of Northern Pike in Shingobee Lake from 2009-2017.Black solid lines represent PSD, grey lines represent PSD-P, and black dashed lines represent PSD-M. Error bars for each indices represents 95% CI.

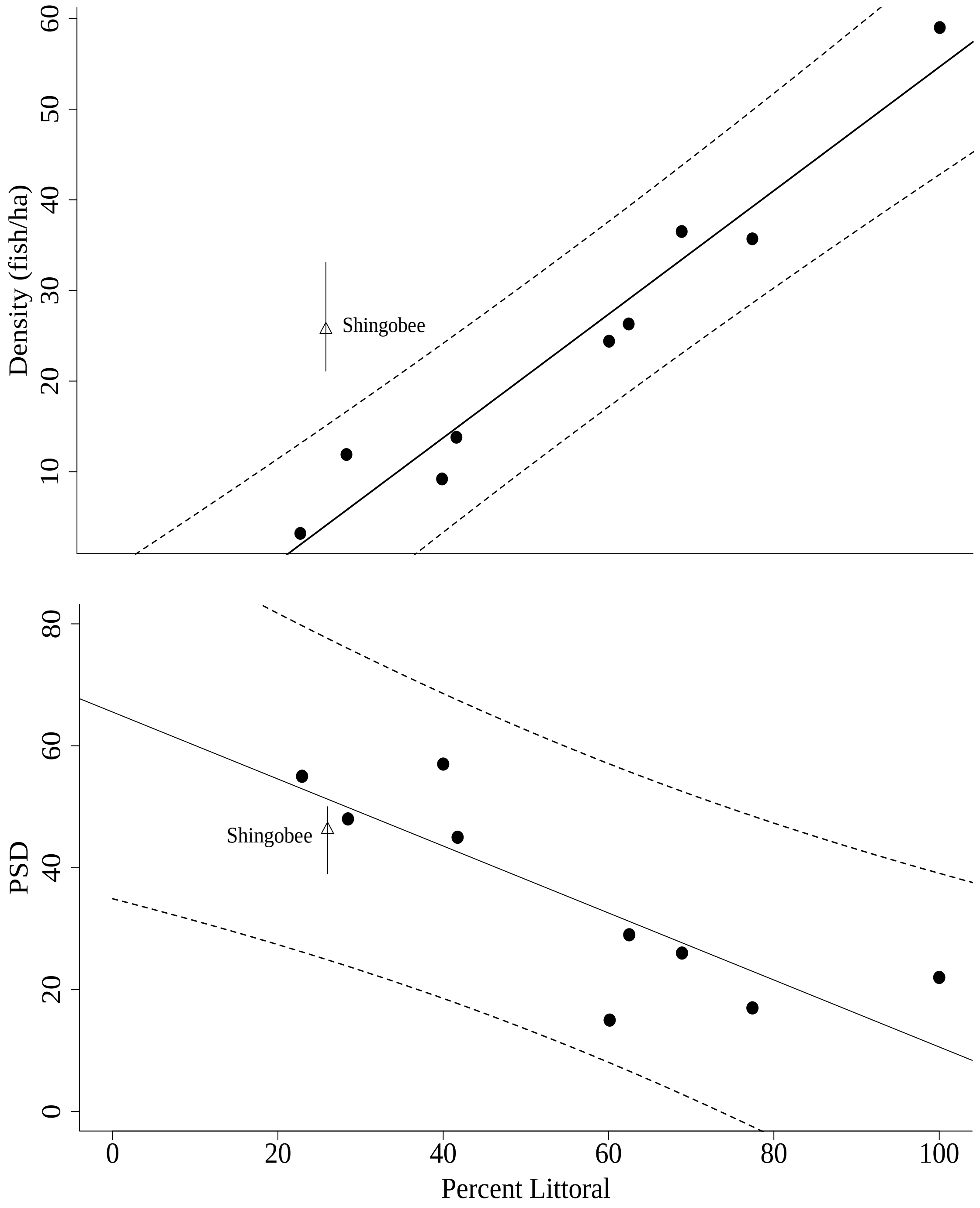

Figure 12. Relationship between percent littoral area and density of Northern Pike from Shingobee Lake and 9 north-central Minnesota lakes (upper panel; bounds represent 95% prediction intervals), and relationship between percent littoral area and Proportional Stock Density (PSD) of the same lakes (lower panel; bounds represent 95% prediction intervals). Shingobee Lake is represented by mean values throughout the study period. Black bars indicate range.